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Retrospective Analysis of Diversity and Species Composition of Marine Macroalgae of Hainan Island (China)

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Abstract – Retrospective analysis of diversity and species composition of marine macroalgae of Hainan Island in the period 1933–1992 is presented in this paper. There are two extensive sample collection periods of benthic macroalgae: the early collection (EC) covers a period between the early 1930s and the 1980s before considerable urbanization and reef degradation took place and a late collection (LC) was performed in 1990/1992 during a phase of rapid urbanization. Analysis of data also including an earlier published inventory of green algae covering the same collection sites (Titlyanov et al. 2011a) revealed that the marine flora of the island comprises 426 taxa in total, with 59% red algae, 18% brown algae and 23% green algae. In total 59 species of red algae, 11 species of brown algae and 37 species of green algae sampled during the LC are new records for Hainan Island. Considerable floristic changes between EC and LC became evident. In the LC there were significantly more filamentous, tubular or fine blade-like, and often epiphytic, green and red algae with a high surface-to-volume ratio. Additionally a reduction of green, brown and red algal species with larger fleshy or foliose thalli and a low surface-to-volume ratio was observed. It is assumed that the changes reflect the degradation of the coral reef ecosystem around Hainan, which was damaged by human activities especially in the 1950s–1970s.

Key words – retrospective analysis, floristic composition, Hainan Island, inventory, macroalgae, morpho-functional groups

1. Introduction

Coral reefs form the major coastal ecosystem in subtropical to tropical intertidal and shallow subtidal zones of exposed and semi-exposed shorelines. Until the middle of the last century, the coastal ecosystems of Hainan Island (South China Sea) had not been subjected to major anthropogenic stress, although coral reefs, mangroves and seagrass meadows of Hainan Island were exploited (Gurianova 1959). During the second half of the 20th century the coral reefs in particular around Hainan Island were subjected to destructive dynamite fishing (Zhao et al. 2008), and coral colonies were used for lime production and pier′ constructions, both of which posed a major physical challenge to this valuable habitat (Hutchings and Wu 1987; Fiege et al. 1994; Hodgson and Yau 1997; Kimura et al. 2008). Furthermore, there was pollution caused by mariculture waste from shrimp or fish ponds (Zhang et al. 2004, 2006; Zhao et al. 2008). Since the 1990s increasing tourist numbers, hotels built directly on the beach and aquaculture industries (pearl shell culture and *Eucheuma* cultivation) have additionally endangered the coastal marine fauna and flora. By 1990/1992, reef degradation and sediment loading already were noticeable (Fiege et al. 1994; Gu and Wall 2007). Recently, almost 80% of the fringing reefs along the coastline of Hainan Island have been destroyed (Hutchings and Wu 1987; Zhang et al. 2006).

Two major algal collection periods covering similar sites, habitats and seasons all over the island were conducted in Hainan Island: early collections (EC) cover a period between the 1930s–1980s before the start of physical degradation, and a late collection (LC) was performed in 1990/1992. We postulate that environmental changes in Hainan Island taking place between these two periods may be reflected by the

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species diversity of green, brown and red benthic macroalgae, and by the occurrence and relative dominance of specific algal groups. Serious changes in the floristic diversity and composition of marine benthic algae in Hainan Island have already been documented in the green algal flora during the last century (Titlyanov et al. 2011a).

In the present study, we compiled comprehensive checklists of marine brown and red seaweeds collected in Hainan Island and nearby islets from the early collections (EC) conducted between the 1930s–1980s and from our collections in 1990/1992, compare the floristic composition between these two collections, and analyze the qualitative changes that have taken place over time with reference to local and global environmental changes.

2. Materials and Methods

Study area and algal collections

Hainan Island (18°10'–20°9'N, 108°37'–11°1'E) is located in the South China Sea, has an area of 33.920 km^2 and a coastline of more than 1,600 km. The annual mean sea surface temperature (SST) is 26°C (1970–2002) (Sun et al. 2005). The annual maximum and minimum SST commonly occurs in July (30.8°C) and January (18.7°C), respectively. Mean sea surface salinity (SSS) in the South China Sea fluctuates between 33.3 and 34.0. However, in Hainan Island, the SSS tends to decrease markedly (min. 26.5) due to the freshwater runoff and heavy rain during the summer wet season (Levitus and Boyer 1994). The mean tidal range is mostly less than 1.5 m (Zhang et al. 1996).

The first comprehensive collections of marine seaweeds in Hainan Island were performed by Tseng and colleagues in 1933 and 1934, which covered many coastal sites all around the island (Fig. 1A). The subsequent algal samplings were carried out at many diverse localities of the island between 1950 and 1980. Material (herbarium sheets) from these samplings were processed by Chinese phycologists and deposited at the herbarium of the Institute of Oceanology of the Chinese Academy of Sciences (Tseng 2004).

All subsequently listed publications have been considered for this paper: Tseng 1935, 1936, 1937, 1938, 1941a, 1941b, 1942a, 1942b, 1983, 2004, 2009; Tseng and Gilbert 1942; Tseng and Chang 1962; Tseng et al. 1962, 1980, 2001, 2011; Chang and Xia 1962, 1963, 1976; Tseng and Dong 1978; Zhang and Xia 1979, 1980, 1981, 1983, 1984, 1988a, 1988b, 1988c, 1991, 1994; Zheng 1980; Zhu and Liu 1980; Xia and Zhang 1982, 1999; Meiling and Tseng 1985; Xia 1985, 2004; Doty and Norris 1985; Xia and Abbott 1985, 1987, 1999; Xia and Yamamoto 1985; Doty 1988; Santelices 1988; Tseng and Lu 1988, 1992, 1995a, 1995b, 1995c, 1997, 1999, 2000, 2002a, 2002b, 2002c, 2002d; Chiang et al. 1992; Masuda et al. 1994; Xia and Wang 1997, 1999, 2000a, 2000b, 2002; Millar and Xia 1999;Tseng and Xia 1999; Xia et al. 2002, 2004a, 2004b; Zeng et al. 2005; Ding et al. 2007; Liu 2008; Zheng and Li 2009. On the basis of these publications, a species list of all seaweed species found in Hainan between 1933 and the 1980s were compiled to represent the EC.

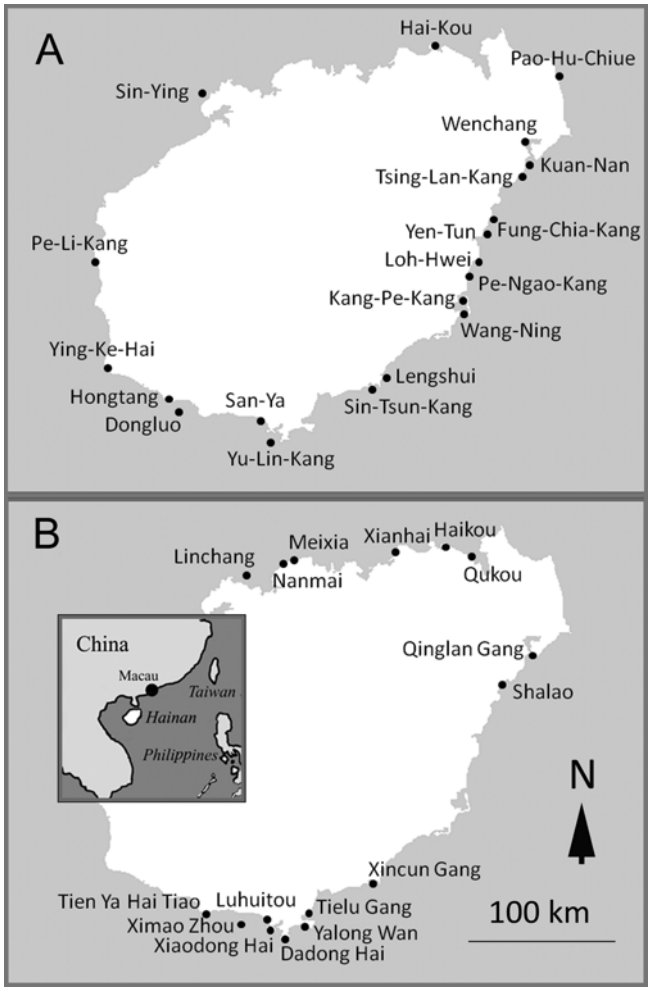

Fig. 1. Hainan Island (South China Sea, China) (1810'-20°9'N, 108°37'-111°1'E). (A) Collection sites of Tseng and co-workers in 1933–1935 with old spellings of names (after Tseng 1936). (B) Collection sites during 1990/1992 (after Titlyanov et al. 2011a)

In October–December 1990 and in March–April 1992,

another comprehensive sampling campaign was carried out at shallow water localities around Hainan (Fig. 1B). These collections were conducted in the framework of two German-Chinese expeditions and are treated as the "late collection" (LC). Herbarium samples from these expeditions are deposited at the Alfred-Wegener-Institute Helmholtz-Centre for Polar and Marine Research (Germany) and at the Institute of Oceanology in Qingdao (China).

The EC was sampled and identified by Chinese phycologists (including one author of the present paper: B. Xia), and the LC was sampled by Chinese and German phycologists (including B. Xia and I. Bartsch). Herbarium samples of the LC were identified by B. Xia in 1990–1994 and by T. Titlyanova and E. Titlyanov in 2007–2009. The specimens of the LC were identified with the help of monographic publications, floristic studies, and taxonomic articles listed in previous publications (Titlyanov et al. 2011a; Titlyanova et al. 2012).

3. Results

Red and brown algal species diversity and compositional changes between EC and LC

In total, 240 taxa (species, their taxonomic forms and varieties) from 35 families of red algae have been collected at Hainan Island since 1933. Liagoraceae (46 taxa), Rhodomelaceae (30), Gracilariaceae (24), Corallinaceae (21), Ceramiaceae (13) Halymeniaceae (11) and Acrochaetiaceae (11) were the dominant families of the Hainan red algal flora. Total taxa of brown algae (75 taxa) only comprised less than one-third of the volume of red algae. Sargassaceae (44) and Dictyotaceae (14) were the dominant families of the brown algal flora (Tables 1, 2).

During EC, 178 red algal taxa were recorded. The majority of species belonged to the families Liagoraceae (46 taxa), Gracilariaceae (21), Rhodomelaceae (18), Corallinaceae (14) and Halymeniaceae (11) (Tables 1, 2; Fig. 2). Sixty-four taxa of brown algae were recorded for Hainan Island during the EC, with the families Sargassaceae (41 taxa) and Dictyotaceae (10) comprising most species (Tables 1, 2; Fig. 2).

During LC, 105 taxa of red algal were recorded which is 41% less than in EC: Rhodomelaceae (17 taxa), Ceramiaceae (13) and Corallinaceae (11) were the dominant families in EC (Tables 1, 2; Fig. 2). Thirty two taxa of brown algae were sampled in 1990/1992 (LC) and thereby only comprised 50% of the EC. Sargassaceae (11 taxa) and Dictyotaceae (11) still contained the greatest number of taxa (Tables 1, 2; Fig. 2).

Thus, species richness and composition of red and brown macroalgae sampled during the EC and LC differed considerably. The LC was much poorer in species diversity than the EC. Collections also differed in taxonomic composition. In LC, species richness was slightly higher in red algae (76%) and slightly lower in brown algae (24%). Eight families of red algae (Bangiaceae, Hapalidiaceae, Sporolithaceae, Phyllophoraceae, Ahnfeltiaceae, Sarcodiaceae, Rhodymeniaceae and Sebdeniaceae) which had been present in EC were not found in LC. At the same time, new records were found for the families Stylonemataceae, Erythrotrichiaceae, Rhizophyllidaceae, Hymenocladiaceae, Callithamniaceae, and Spyridiaceae during LC. The EC was dominated by red algae from the families Liagoraceae and Gracilariaceae, while the LC was dominated by red algae from the families Rhodomelaceae and Ceramiaceae. In brown algae, in the both collections most species were from the families Sargassaceae and Dictyotaceae. Fig. 2 comparatively shows the difference in species number of red and brown algae of species rich families in the EC and LC, reflecting changes in the flora during the two sampling periods. During LC, among red algae species the number decreased in the families Acrochaetiaceae, Corallinaceae, Cystocloniaceae, Galaxauraceae, Gracilariaceae, Halymeniaceae, Liagoraceae, Scinaiaceae, Solieriaceae, Wrangeliaceae and the number of species of brown algae decreased in the families Acinetosporaceae, Sargassaceae and Scytosiphonaceae. At the same time the number of red algae increased in the families Ceramiaceae, Colaconemataceae and Erythrotrichiaceae.

Fig. 3 shows that 19% of red algal species and 28% of brown algal species were common to both collection periods. In 1990/1992, 56% of red algal taxa and 57% of brown algal taxa which had been recorded during EC were not recorded again. The largest number of taxa that were not re-found in LC became apparent in the families of red macroalgae: Liagoraceae (41 taxa) and Gracilariaceae (17); in the families of brown macroalgae - the Sargassaceae (33 taxa) (Tables 1, 2). Fifty nine species of red algae (or 24% of all taxa recorded since 1933) have been newly documented for Hainan Island in LC (Tables 1, 2, 3; Fig. 3). These new records represent 56% of all species recorded during LC. The highest number of new records was in the families Ceramiaceae (12), Rhodomelaceae (10) and Corallinaceae (7) (Tables 2, 3). Eleven brown algal species (14% of all taxa recorded since 1933 or 34% of species found during LC) were recorded for

Table 1. List of species (including varieties and forms) of the marine flora (Rhodophyta and Phaeophyceae) for Hainan Island (China)

Taxon	EC (1930s–1970s)	LC 1990, 1992
1	2	3
Rhodophyta		
Order BANGIALES		
Family BANGIACEAE		
Porphyra crispata Kjellman	+	
Pyropia vietnamensis (T. Tanaka & P.H. Ho) J.E. Sutherland & Monotilla	+	
Order STYLONEMATALES		
Family STYLONEMATACEAE		
Stylonema alsidii (Zanardini) K.M. Drew*		+
Chroodactylon ornatum (C. Agardh) Basson*		+
Order ERYTHROPELTIDALES		
Family ERYTHROTRICHIACEAE		
Erythrotrichia carnea (Dillwyn) J. Agardh*		+
Erythrocladia irregularis Rosenvinge*		+
Porphyrostromium japonicum (Tokida) Kikuchi*		+
Sahlingia subintegra (Rosenvinge) Kornmann*		+
Order ACROCHAETIALES		
Family ACROCHAETIACEAE		
Acrochaetium globosum Børgesen	+	
Acrochaetium macula (Rosenvinge) G. Hamel	+	
Acrochaetium microscopicum (Nägeli ex Kützing) Nägeli	+	+
Acrochaetium netrocarpum Børgesen	+	
Acrochaetium robustum Børgesen	+	+
Acrochaetium ryukyuense (Nakamura) Papenfuss	+	
Acrochaetium secundatum (Lyngbye) Nägeli*		+
Acrochaetium subseriatum Børgesen*		+
Acrochaetium virgatulum (Harvey) Batters*		+
Acrochaetium yamadae (Garbary) Y. Lee & I.K. Lee	+	
Order COLACONEMATALES		
Family COLACONEMATACEAE		
Colaconema bonnemaisoniae Batters*		+
Colaconema daviesii (Dillwyn) Stegenga*		+
Colaconema dictyotae (Collins) I.-K. Hwang & H.-S. Kim	+	
Colaconema gracile (Børgesen) Ateweberhan & Prud'homme van Reine	+	+
Colaconema *hypneae* (Børgesen) A.A. Santos & C.W.N. Moura	+	+
Order NEMALIALES		
Family GALAXAURACEAE		
Actinotrichia fragilis (Forsskål) Børgesen	+	+
Dichotomaria apiculata (Kjellman) Kurihara & Masuda	+	
Dichotomaria falcata (Kjellman) Kurihara & Masuda*		+
Dichotomaria marginata (J. Ellis & Solander) Lamarck	+	
Dichotomaria spathulata (Kjellman) A. Kurihara & Huisman	+	+
Galaxaura divaricata (Linnaeus) Huisman & R.A. Townsend	+	
Galaxaura filamentosa R.C.Y. Chou	+	
Galaxaura rugosa (J. Ellis & Solander) J.V. Lamouroux	+	
Tricleocarpa fragilis (Linnaeus) Huisman & R.A. Townsend	+	+

Table 1. Continued

Taxon	EC (1930s–1970s)	LC 1990, 1992
1	2	3
Family LIAGORACEAE		
Dermonema pulvinatum (Grunow ex Holmes) Fan	+	+
Dermonema virens (J. Agardh) Pedroche & Ávila Ortíz	+	
Dotyophycus hainanensis Tseng & Li	+	
Ganonema farinosa (Lamouroux) Fan et Wang	+	+
Ganonema papenfussii (I.A. Abbott) J.M. Huisman, I.A. Abbott, & A.R. Sherwood	+	
Ganonema *pinnatiramosa* (*Yamada*) K.C. Fan & Y.C. Wang	+	
Ganonema pinnatum (Harvey) Huisman	+	
Ganonema samaense (C.K. Tseng) Huisman	+	
Helminthocladia australis Harvey	+	
Helminthocladia hainanensis Tseng & Li	+	
Helminthocladia pinnata Tseng & Li	+	
Izziella formosana (Yamada) S.M. Lin, S.-Y. Yang & Huisman	+	
Izziella orientalis (J. Agardh) Huisman & Schils	+	+
Liagora albicans J.V. Lamouroux	+	
Liagora boergesenii Yamada	+	
Liagora ceranoides J.V. Lamouroux	+	+
Liagora clavata Yamada	+	
Liagora dongdaoensis Tseng & Li	+	
Liagora fanii Tseng & Li	+	
Liagora filiformis Fan & Li	+	
Liagora hainanensis C. K. Tseng & Li	+	
Liagora paniculata Tseng & Li	+	
Liagora qishuiwanensis Li	+	
Liagora rhizophora Tseng & Li	+	
Liagora robusta Yamada	+	
Liagora rubra C.K. Tseng & Li	+	
Liagora segawae Yamada	+	
Liagora sinensis K.C. Fan, Y.C. Wang & K.Y. Pan	+	
Liagora subdichotoma Tseng & Li	+	
Liagora wenchangensis Tseng & Li	+	
Liagora wilsoniana Zeh	+	
Macrocarpus perennis (I.A. Abbott) S.M. Lin, S.-Y. Yang & Huisman	+	
Neoizziella divaricata (C.K. Tseng) S.M. Lin, S.-Y. Yang & Huisman	+	
Sinocladia divergenscata C.K. Tseng & W. Li	+	
Sinocladia dongjiaoensis C.K. Tseng & W. Li	+	
Sinocladia flabelliformis C.K. Tseng & W. Li	+	
Sinocladia hainanensis C.K. Tseng & W. Li	+	
Sinocladia paniculata C.K. Tseng & W. Li	+	
Sinocladia pinnata C.K. Tseng & W. Li	+	
Sinocladia qionghaiensis C.K. Tseng & W. Li	+	
Sinocladia ramosissima C.K. Tseng & W. Li	+	
Titanophycus setchellii (Yamada) S.-M. Lin, S.-Y. Yang & Huisman	+	
Titanophycus validus (Harvey) Huisman, G.W. Saunders & A.R. Sherwood	+	
Trichogloeopsis hawaiiana I.A. Abbott & Doty	+	
Trichogloeopsis mucosissima (Yamada) I.A. Abbott & Doty	+	+
Yamadaella caenomyce (Decaisne) I.A. Abbott	+	

Table 1. Continued

Taxon	EC (1930s–1970s)	LC 1990, 1992
1	2	3
Family SCINAIACEAE		
Scinaia boergesenii C.K. Tseng	+	+
Scinaia chinensis (C.K. Tseng) Huisman	+	+
Scinaia latifrons M.A. Howe	+	
Scinaia tsinglanensis C.K. Tseng	+	
Order GELIDIALES		
Family GELIDIACEAE		
Gelidium crinale (Hare ex Turner) Gaillon*		+
Gelidium divaricatum G. Martens*		+
Gelidium pusillum (Stackhouse) Le Jolis	+	+
Gelidium pusillum var. *cylindricum* W.R. Taylor	+	+
Gelidium pusillum var. *pacificum* W.R. Taylor	+	
Family GELIDIELLACEAE		
Gelidiella acerosa (Forsskål) Feldmann & G. Hamel	+	+
Gelidiella bornetii (Weber-van Bosse) Feldmann & C. Hamel (Hainan)	+	+
Gelidiella lubrica (Kützing) Feldmann & G. Hamel*		+
Parviphycus adnatus (E.Y. Dawson) B. Santelices*		+
Parviphycus pannosus (Feldmann) G. Furnari*		+
Family PTEROCLADIACEAE		
Pterocladiella caerulescens (Kützing) Santelices & Hommersand	+	
Pterocladiella capillacea (S.G. Gmelin) Santelices & Hommersand		+
Pterocladiella yinggehaiensis B.M. Xia & C.K. Tseng	+	
Order BONNEMAISONIALES		
Family BONNEMAISONIACEAE		
Asparagopsis taxiformis (Delile) Trevisan de Saint-Léon	+	+
Order HALYMENIALES		
Family HALYMENIACEAE		
Carpopeltis maillardii (Montagne & Millardet) Chiang	+	
Cryptonemia basinervis B.M. Xia & Wang	+	
Cryptonemia seminervis (C. Agardh) J. Agardh	+	
Cryptonemia xinhaiensis B.M. Xia & Wang	+	
Halymenia maculata J. Agardh	+	+
Grateloupia hainanensis W.-X. Li & Z.-F. Ding	+	
Grateloupia kurogii Kawaguchi	+	
Grateloupia livida (Harvey) Yamada	+	
Grateloupia ramosissima Okamura	+	
Isabbottia ovalifolia (Kylin) Balakrishnan	+	
Yonagunia formosana (Okamura) Kawaguchi & Masuda	+	+
Order PEYSSONNELIALES		
Family PEYSSONNELIACEAE		
Peyssonnelia conchicola Piccone & Grunow	+	
Peyssonnelia orientalis (Weber-van Bosse) Cormaci & G. Furnari	+	+
Order CORALLINALES		
Family CORALLINACEAE		
Amphiroa anastomosans Weber-van Bosse	+	
Amphiroa foliacea J.V. Lamouroux*		+

Table 1. Continued

Taxon	EC (1930s–1970s)	LC 1990, 1992
1	2	3
Amphiroa fragilissima (Linnaeus) J.V. Lamouroux	+	+
Amphiroa fragilissima f. *cyathifera* (J.V. Lamouroux) Weber-van Bosse	+	+
Hydrolithon boreale (Foslie) Y.M. Chamberlain*		+
Hydrolithon farinosum (J.V. Lamouroux) D. Penrose & Y.M. Chamberlain*		+
Hydrolithon onkodes (Heydrich) D. Penrose & Woelkerling	+	
Hydrolithon reinboldii (Weber-van Bosse & Foslie) Foslie	+	
Jania acutiloba (Decaisne) J.H. Kim, Guiry & H.-G. Choi	+	+
Jania adhaerens J.V. Lamouroux	+	+
Jania capillacea Harvey*		+
Jania crassa J.V. Lamouroux	+	
Jania pumila J.V. Lamouroux*		+
Jania ungulata f. *brevior* (Yendo) Yendo*		+
Jania verrucosa J.V. Lamouroux	+	
Mastophora pacifica (Heydrich) Foslie	+	
Mastophora rosea (C. Agardh) Setchell	+	
Lithophyllum kotschyanum Unger	+	
Lithophyllum pygmaeum (Heydrich) Heydrich	+	
Lithoporella melobesioides (Foslie) Foslie	+	
Pneophyllum fragile Kützing*		+
Family HAPALIDIACEAE		
Mesophyllum mesomorphum (Foslie) Adey	+	
Order SPOROLITHALES		
Family SPOROLITHACEAE		
Sporolithon erythraeum (Rothpletz) Kylin	+	
Order GIGARTINALES		
Family CYSTOCLONIACEAE		
Hypnea boergesenii T. Tanaka	+	
Hypnea charoides J.V. Lamouroux	+	+
Hypnea cornuta (Kützing) J. Agardh	+	+
Hypnea japonica Tanaka	+	
Hypnea musciformis var. *esperi* J. Agardh*		+
Hypnea pannosa J. Agardh	+	+
Hypnea spinella (C. Agardh) Kützing	+	+
Family SOLIERIACEAE		
Betaphycus gelatinum (Esper) Doty ex P.C. Silva	+	+
Eucheuma edule (Kützing) Weber-van Bosse	+	
Eucheuma serra (J. Agardh) J. Agardh	+	
Kappaphycus alvarezii (Doty) Doty ex P.C. Silva	+	
Kappaphycus cottonii (Weber-van Bosse) Doty ex P.C. Silva	+	
Sarconema filiforme (Sonder) Kylin	+	
Sarconema gracilarioides Zhang & E.Z. Xia	+	
Solieria pacifica (Yamada) Yoshida	+	
Wurdemannia miniata (Sprengel) Feldmann & G. Hamel	+	
Family PHYLLOPHORACEAE		
Ahnfeltiopsis flabelliformis (Harvey) Masuda	+	
Ahnfeltiopsis hainanensis B.-M. Xia & Y.-Q. Zhang	+	
Ahnfeltiopsis pygmaea (J. Agardh) P.C. Silva & DeCew	+	

Table 1. Continued

Taxon	EC (1930s–1970s)	LC 1990, 1992
1	2	3
Family RHIZOPHYLLIDACEAE		
Portieria hornemannii (Lyngbye) P.C. Silva*		+
Order AHNFELTIALES		
Family AHNFELTIACEAE		
Ahnfeltia yinggehaiensis B.-M. Xia & Y.-Q. Zhang	+	
Order PLOCAMIALES		
Family SARCODIACEAE		
Sarcodia montagneana (J.D. Hooker & Harvey) J. Agardh	+	
Trematocarpus pygmaeus Yendo	+	
Order RHODYMENIALES		
Family CHAMPIACEAE		
Champia parvula (C. Agardh) Harvey*		+
Champia vieillardii Kützing*		+
Coelothrix irregularis (Harvey) Børgesen	+	
Family LOMENTARIACEAE		
Ceratodictyon intricatum (C. Agardh) R.E. Norris	+	+
Ceratodictyon spongiosum Zanardini	+	+
Lomentaria corallicola Børgesen*		+
Family RHODYMENIACEAE		
Rhodymenia hainanensis B.-M. Xia & Y.-Q. Zhang	+	
Family HYMENOCLADIACEAE		
Asteromenia anastomosans (Weber-van Bosse) G.W. Saunders, C.E. Lane, C.W. Schneider & Kraft*		+
Order SEBDENIALES		
Family SEBDENIACEAE		
Sebdenia flabellata (J. Agardh) P.G. Parkinson	+	
Order GRACILARIALES		
Family GRACILARIACEAE		
Gracilaria arcuata Zanardini	+	
Gracilaria articulata C.F. Chang & B.M. Xia	+	
Gracilaria blodgettii Harvey	+	
Gracilaria bursa-pastoris (Gmelin) P.S. Silva	+	
Gracilaria canaliculata (Kützing) Sonder	+	
Gracilaria changii (B.M. Xia & I.A. Abbott) I.A. Abbott, J. Zhang & B.M. Xia*		+
Gracilaria chondracantha (Kützing) Millar	+	
Gracilaria chorda Holmes		
Gracilaria compressa (C. Agardh) Greville		
Gracilaria coronopifolia J. Agardh		+
Gracilaria cuneifolia (Okamura) I.K. Lee & Kurogi	+	+
Gracilaria glomerata Zhang & B.M. Xia	+	
Gracilaria hainanensis C.F. Chang & B.M. Xia	+	
Gracilaria rubra (C. Agardh) J. Agardh	+	
Gracilaria salicornia (C. Agardh) E.Y. Dawson	+	+
Gracilaria spinulosa (Okamura) Chang & B.M. Xia	+	
Gracilaria tenuistipitata var. *liui* Zhang & Xia	+	+
Gracilaria yamamotoi Zhang & B.M. Xia	+	
Gracilariopsis heteroclada J.F. Zhang & B.M. Xia	+	+

Table 1. Continued

Taxon	EC (1930s–1970s)	LC 1990, 1992
1	2	3
Gracilariocolax deformans (Weber van Bosse) Gerung & Yamamoto	+	
Gracilariocolax henriettae Weber van Bosse	+	
Gracilariocolax infidelis (Weber van Bosse) Gerung & Yamamoto	+	
Gracilariocolax setchellii (Weber van Bosse) Gerung & Yamamoto	+	
Hydropuntia edulis (S.G. Gmelin) Gurgel & Fredericq	+	+
Hydropuntia eucheumatoides (Harvey) Gurgel & Fredericq	+	+
Order CERAMIALES		
Family CALLITHAMNIACEAE		
Crouania attenuata (C. Agardh) J. Agardh*		+
Family CERAMIACEAE		
Antithamnion antillanum Børgesen*		+
Antithamnionella spirographidis (Schiffner) E.M. Wollaston*		+
Centroceras clavulatum (C. Agardh) Montagne	+	+
*Centroceras minutum*Yamada*		+
Ceramium aduncum Nakamura*		+
Ceramium borneense Weber-van Bosse*		+
Ceramium cingulatum Weber-van Bosse*		+
Ceramium macilentum J. Agardh*		+
Ceramium tenerrimum (G. Martens) Okamura*		+
Ceramium vagans P.C. Silva*		+
Corallophila kleiwegii Weber-van Bosse*		+
Gayliella flaccida (Harvey ex Kützing) T.O. Cho & L.J. McIvor*		+
Family DELESSERIACEAE		
Acrosorium ciliolatum (Harvey) Kylin	+	
Taenioma perpusillum (J. Agardh) J. Agardh*		+
Family RHODOMELACEAE		
Acanthophora muscoides (Linnaeus) Bory de Saint-Vincent	+	
Acanthophora spicifera (M. Vahl) Børgesen	+	+
Acrocystis nana Zanardini	+	
Amansia glomerata C. Agardh	+	
Bostrychia tenella (J.V. Lamouroux) J. Agardh	+	+
Chondria armata (Kützing) Okamura	+	+
Chondria repens Børgesen*		+
Chondrophycus cartilagineus (Yamada) Garbary & Harper	+	+
Chondrophycus undulatus (Yamada) Garbary & Harper	+	
Herposiphonia parca Setchell*		+
Herposiphonia secunda (C. Agardh) Ambronn*		+
Herposiphonia secunda f. *tenella* (C. Agardh) M.J. Wynne*		+
Laurencia majuscula (Harvey) A.H.S. Lucas	+	
Laurencia mariannensis Yamada	+	
Laurencia okamurae Yamada	+	
Laurencia similis Nam & Saito	+	
Laurencia tropica Yamada	+	
Leveillea jungermannioides (K. Hering & G. Martens) Harvey	+	+
Lophosiphonia reptabunda (Suhr) Kylin*		+
Neosiphonia ferulacea (Suhr ex J. Agardh) S.M. Guimarães & M.T. Fujii*		+

Table 1. Continued

Taxon	EC (1930s–1970s)	LC 1990, 1992
1	2	3
Neosiphonia harlandii (Harvey) M.S. Kim & I.K. Lee	+	
Neosiphonia harveyi (J. Bailey) M.-S. Kim, H.-G. Choi, Guiry & G.W. Saunders	+	
Neosiphonia sphaerocarpa (Børgesen) M.S. Kim & I.K. Lee	+	+
Neosiphonia tongatensis (Harvey ex Kützing) M. S. Kim & I.K. Lee	+	+
Palisada parvipapillata (C.K. Tseng) K.W. Nam		+
Palisada *perforata* (Bory de Saint-Vincent) K.W. Nam*		+
Polysiphonia blandii Harvey		
Polysiphonia crassa Okamura		
Polysiphonia scopulorum Harvey*		+
Polysiphonia scopulorum var. *villum* (J. Agardh) Hollenberg*		+
Polysiphonia subtilissima Montagne*		+
Tolypiocladia condensata (Weber-van Bosse) P.C. Silva*		+
Tolypiocladia glomerulata (C. Agardh) F. Schmitz		+
Family WRANGELIACEAE		
Anotrichium tenue (C. Agardh) Nägeli	+	+
Gordoniella yonakuniensis (Yamada & T. Tanaka) Itono*		+
Griffithsia heteromorpha Kützing	+	
Griffithsia metcalfii C.K. Tseng	+	
Griffithsia metcalfii f. *subsecunda* C.K. Tseng	+	
Griffithsia subcylindrica Okamura	+	
Wrangelia argus (Montagne) Montagne*		+
Wrangelia hainanensis C.K. Tseng	+	+
Family SPYRIDIACEAE		
Spyridia filamentosa (Wulfen) Harvey		+
OCHROPHYTA		
Order SCYTOTHAMNALES		
Family SCYTOTHAMNACEAE		
Asteronema breviarticulatum (J. Agardh) Ouriques & Bouzon*		+
Asteronema rhodochortonoides (Børgesen) D.G. Müller & E.R. Parodi	+	
Order ECTOCARPALES		
Family ACINETOSPORACEAE		
Ectocarpus simpliciusculus C. Agardh	+	
Ectocarpus tamarinii Børgesen	+	
Feldmannia irregularis (Kützing) G. Hamel*		+
Feldmannia mitchelliae (Harvey) H.-S. Kim	+	+
Hincksia conifera (Børgesen) I.A. Abbott	+	
Kuetzingiella elachistaeformis (Heydrich) M. Balakrishnan & Kinkar	+	
Order SCYTOSIPHONALES		
Family SCYTOSIPHONACEAE		
Chnoospora implexa J. Agardh	+	+
Chnoospora minima (K. Hering) Papenfuss	+	
Colpomenia sinuosa (Mertens ex Roth) Derbès & Solier	+	+
Hydroclathrus clathratus (C. Agardh) M.A. Howe	+	+
Rosenvingea intricata (J. Agardh) Børgesen	+	+
Rosenvingea orientalis (J. Agardh) Børgesen	+	

Table 1. Continued

Taxon	EC (1930s–1970s)	LC 1990, 1992
1	2	3
Order SPHACELARIALES		
Family SPHACELARIACEAE		
Sphacelaria novae-hollandiae Sonder*		+
Sphacelaria rigidula Kützing*		+
Sphacelaria tribuloides Meneghini	+	+
Order DICTYOTALES		
Family DICTYOTACEAE		
Canistrocarpus cervicornis (Kützing) De Paula & De Clerck	+	+
Dictyopteris repens (Okamura) Børgesen*		+
Dictyota bartayresiana J.V. Lamouroux*		+
Dictyota dichotoma (Hudson) J.V. Lamouroux	+	
Dictyota dichotoma var. *intricata* (C. Agardh) Greville		+
Dictyota friabilis Setchell	+	+
Dictyota implexa (Desfontaines) J.V. Lamouroux	+	+
Lobophora variegata (J.V. Lamouroux) Womersley ex Oliveira	+	+
Padina antillarum (Kützing) Piccone	+	
Padina australis Hauck	+	+
Padina boryana Thivy	+	+
Padina jonesii Tsuda*		+
Padina minor Yamada	+	+
Padina tetrastromatica Hauck	+	
Order FUCALES		
Family SARGASSACEAE		
Hormophysa cuneiformis (J.F. Gmelin) P.C. Silva	+	
Sargassum agaviforme Tseng & Lu*		+
Sargassum aquifolium (Turner) C. Agardh	+	+
Sargassum baccularia (Mertens) C. Agardh	+	
Sargassum carpophyllum J. Agardh	+	
Sargassum cervicorne Greville	+	
Sargassum cinctum J. Agardh	+	
Sargassum crispifolium Yamada	+	
Sargassum cystophyllum var. *parcespinosa* Grunow	+	
Sargassum dazhouense Tseng & Lu	+	
Sargassum dotyi Trono	+	
Sargassum erumpens Tseng & Lu	+	
Sargassum euryphyllum (Grunow) Tseng & Lu	+	
Sargassum feldmannii Pham-Hoàng Hô	+	
Sargasssum glaucescens J. Agardh	+	
Sargassum granuliferum C. Agardh	+	
Sargassum hainanense Tseng & Lu	+	
Sargassum hemiphyllum (Turner) C. Agardh*		+
Sargassum henslowianum C. Agardh*		+
Sargassum herklotsii Setchell	+	+
Sargassum ilicifolium (Turner) C. Agardh	+	+
Sargassum ilicifolium var. *conduplicatum* Grunow	+	
Sargassum intermedium Tseng & Lu	+	

Table 1. Continued

Taxon	EC (1930s–1970s)	LC 1990, 1992
1	2	3
Sargassum mcclurei Setchell	+	
Sargassum megalocystum Tseng & Lu	+	
Sargassum oligocystum Montagne	+	+
Sargassum parvifolium (Turner) C. Agardh	+	
Sargassum phyllocystum Tseng & Lu	+	
Sargassum polycystum C. Agardh	+	+
Sargassum primitivum Tseng & Lu	+	
Sargassum pseudolanceolatum Tseng & Lu	+	
Sargassum qionghaiense Tseng & Lu	+	
Sargassum sanyaense Tseng & Lu	+	
Sargassum siliquosum J. Agardh	+	
Sargassum silvai Tseng & Lu	+	
Sargassum spinifex C. Agardh	+	
Sargassum swartzii C. Agardh	+	+
Sargassum symphyorhizoideum Tseng & Lu	+	
Sargassum tenerrimum J. Agardh	+	+
Sargassum wenchangense Tseng & Lu	+	
Sargassum yinggehaiense Tseng & Lu	+	
Turbinaria conoides (J. Agardh) Kützing	+	
Turbinaria ornata (Turner) J. Agardh	+	+
Turbinaria ornata f. *hainanensis* W.R. Taylor	+	

Annotation: + - The presence of species, * - New records of brown and red algae for Hainan Island.

the first time in LC. The highest number of new records was in the family Dictyotaceae (4) (Tables 2, 3; Fig. 3).

4. Discussion

Inventory of the marine flora of Hainan Island

The species inventory for Hainan Island derived from all published evidence since 1933 and the current data revealed a species richness of 426 taxa of red, brown and green macroalgae in total. This is very similar to the species richness of the neighboring island Taiwan, where over 400 seaweed species were recorded (Lewis and Norris 1987). Not only the species richness but also the relative contribution of red, brown and green algae to the seaweed flora is very similar between both islands. While for Hainan Island 59% Rhodophyta, 23% Chlorophyta, and 18% Phaeophyceae have been recorded, for Taiwan this relation is 55%, 24% and 21%, respectively, and this is also similar to the southern coasts of China (56%, 23% and 19%, respectively) (Lewis and Norris 1987; Zhang 1996). In general the seaweed flora of Hainan Island is thus a typical example of a tropical to subtropical coral reef based island environment and also comparable to other tropical/subtropical islands and continental coasts of the Indo-Pacific region with comparable habitats. In general these areas contain 50–60% Rhodophyta, 20–30% Chlorophyta and 10–20% Phaeophyceae (Womersley 1981; Lewis and Norris 1987; Silva et al. 1987; Silva 1992; Huisman and Borowitzka 2003; Tsuda 2003, 2006).

Prerequisites for comparing algal sampling collections

Comparison of species richness and composition derived from two or more algal collections has been undertaken worldwide in order to identify changes over decadal time scales in the marine flora associated with long-term climate changes, or the influence of anthropogenic factors (e.g. Svane and Gröndahl 1988; Munda 1993; Schories et al. 1997; Eriksson et al. 1998, 2002; Johansson et al. 1998; Sagarin et al. 1999; Bartsch and Kuhlenkamp 2000; Piriz et al. 2003; Schiel et al. 2004; Lima et al. 2007; Tribolett and Vroom 2007; Hawkins et al. 2008; Kinzie 2008; Barrett et al. 2009; Mumby 2009; Vroom and Timmers 2009; Schutte et al. 2010; Trowbridge et al. 2011, 2013). From these four following

Table 2. Numbers of red and brown algal species in different families collected in Hainan Island during different periods and the comparison of species recorded during the early collection period (1930s–1970s) and the late collection (1990/1992)

Familes	Numbers of species					
	EC+LC	EC	LC	Com	New	Lost
RHODOPHYTA						
Bangiaceae	2	2	0	0	0	2
Stylonemataceae	2	0	2	0	2	0
Erythrotrichiaceae	4	0	4	0	4	0
Acrochaetiaceae	11	7	6	2	4	5
Colaconemataceae	5	3	4	2	2	1
Galaxauraceae	9	8	4	3	1	5
Liagoraceae	46	46	5	5	0	41
Scinaiaceae	4	4	2	2	0	2
Gelidiaceae	5	3	4	2	2	1
Gelidiellaceae	5	2	5	2	3	0
Pterocladiaceae	3	2	1	0	1	2
Bonnemaisoniaceae	1	1	1	1	0	0
Halymeniaceae	11	11	2	2	0	9
Peyssonneliaceae	2	2	1	1	0	1
Corallinaceae	21	14	11	4	7	10
Hapalidiaceae	1	1	0	0	0	1
Sporolithaceae	1	1	0	0	0	1
Cystocloniaceae	7	6	5	4	1	2
Solieriaceae	9	9	1	1	0	8
Phyllophoraceae	3	3	0		0	3
Rhizophyllidaceae	1	0	1		1	0
Ahnfeltiaceae	1	1	0	0	0	1
Sarcodiaceae	2	2	0	0	0	2
Champiaceae	3	1	2	0	2	1
Lomentariaceae	3	2	3	2	1	0
Rhodymeniaceae	1	1	0	0	0	1
Hymenocladiaceae	1	0	1	0	1	0
Sebdeniaceae	1	1	0	0	0	1
Gracilariaceae	24	21	6	6	1	17
Callithamniaceae	1	0	1	0	1	0
Ceramiaceae	13	1	13	1	12	0
Delesseriaceae	2	1	1	0	1	1
Rhodomelaceae	30	18	17	7	10	13
Wrangeliaceae	8	6	4	1	2	4
Spyridiaceae	1	1	1	1	0	0
Total (Rhodophyta)	241	178	105	47	59	135
OCHROPHYTA						
Scytothamnaceae	2	1	1	0	1	1
Acinetosporaceae	6	5	2	1	1	4
Scytosiphonaceae	6	6	4	4	0	2
Sphacelariaceae	3	1	3	1	2	0
Dictyotaceae	14	10	11	7	4	3
Sargassaceae	44	41	11	8	3	33
Total (Ochrophyta)	75	64	32	21	11	43

EC, early collection period (1930s–1970s); LC, late collection (1990/1992); Com, common species for the both early and late collections; New, newly recorded species in 1990/1992; Lost, species not found in 1990/1992

Table 3. List of new recorded species of red and brown algae from Hainan Island collected in 1990 and 1992

Taxon	Taxon
RHODOPHYTA	**Gracilariales**
Stylonematales	**Gracilariaceae**
Stylonemataceae	*Gracilaria changii* (B.M. Xia & I.A. Abbott) I.A. Abbott, J. Zhang & B.M. Xia
Stylonema alsidii (Zanardini) K.M. Drew	**Ceramiales**
Chroodactylon ornatum (C. Agardh) Basson	**Callithamniaceae**
Erythropeltidales	*Crouania attenuata* (C. Agardh) J. Agardh
Erythrotrichiaceae	**Ceramiaceae**
Erythrotrichia carnea (Dillwyn) J. Agardh	*Antithamnion antillanum* Børgesen
Erythrocladia irregularis Rosenvinge	*Antithamnionella spirographidis* (Schiffner) E.M. Wollaston
Porphyrostromium japonicum (Tokida) Kikuchi	*Centroceras minutum*Yamada
Sahlingia subintegra (Rosenvinge) Kornmann	*Ceramium aduncum* Nakamura
Acrochaetiales	*Ceramium borneense* Weber-van Bosse
Acrochaetiaceae	*Ceramium cimbricum* H.E. Petersen
Acrochaetium catenulatum M.A. Howe	*Ceramium cingulatum* Weber-van Bosse
Acrochaetium secundatum (Lyngbye) Nägeli	*Ceramium macilentum* J. Agardh
Acrochaetium subseriatum Børgesen	*Ceramium tenerrimum* (G. Martens) Okamura
Colaconematales	*Ceramium vagans* P.C. Silva
Colaconemataceae	*Corallophila kleiwegii* Weber-van Bosse
Colaconema bonnemaisoniae Batters	*Gayliella flaccida* (Harvey ex Kützing) T.O. Cho & L.J. McIvor
Colaconema daviesii (Dillwyn) Stegenga	**Delesseriaceae**
Nemaliales	*Taenioma perpusillum* (J. Agardh) J. Agardh
Galaxauraceae	**Rhodomelaceae**
Dichotomaria falcata (Kjellman) Kurihara & Masuda	*Chondria repens* Børgesen
Gelidiales	*Herposiphonia parca* Setchell
Gelidiaceae	*Herposiphonia secunda* (C. Agardh) Ambronn
Gelidium crinale (Hare ex Turner) Gaillon	*Herposiphonia secunda* f. *tenella* (C. Agardh) M.J. Wynne
Gelidium divaricatum G. Martens	*Lophosiphonia reptabunda* (Suhr) Kylin
Gelidiellaceae	*Neosiphonia ferulacea* (Suhr ex J. Agardh) S.M. Guimarães & M.T. Fujii
Gelidiella lubrica (Kützing) Feldmann & G. Hamel	*Polysiphonia scopulorum* Harvey
Parviphycus adnatus (E.Y. Dawson) B. Santelices	*Polysiphonia scopulorum* var. *villum* (J. Agardh) Hollenberg
Parviphycus pannosus (Feldmann) G. Furnari	*Polysiphonia subtilissima* Montagne
Pterocladiaceae	*Tolypiocladia condensata* (Weber-van Bosse) P.C. Silva
Pterocladiella capillacea (S.G. Gmelin) Santelices & Hommersand	**Wrangeliaceae**
Corallinales	*Gordoniella yonakuniensis* (Yamada & T. Tanaka) Itono
Corallinaceae	*Wrangelia argus* (Montagne) Montagne
Amphiroa foliacea J.V. Lamouroux	**OCHROPHYTA**
Hydrolithon boreale (Foslie) Y.M. Chamberlain	**Scytothamnales**
Hydrolithon farinosum (J.V. Lamouroux) D. Penrose & Y.M. Chamberlain	**Asteronemataceae**
Jania capillacea Harvey	*Asteronema breviarticulatum* (J. Agardh) Ouriques & Bouzon
Jania pumila J.V. Lamouroux	**Ectocarpales**
Jania ungulata f. *brevior* (Yendo) Yendo	**Acinetosporaceae**
Pneophyllum fragile Kützing	*Feldmannia irregularis* (Kützing) G. Hamel
Gigartinales	**Sphacelariales**
Cystocloniaceae	**Sphacelariaceae**
Hypnea musciformis var. *esperi* J. Agardh	*Sphacelaria novae-hollandiae* Sonder
Rhizophyllidaceae Family	*Sphacelaria rigidula* Kützing
Portieria hornemannii (Lyngbye) P.C. Silva	**Dictyotales**
Rhodymeniales	**Dictyotaceae**
Champiaceae	*Dictyopteris repens* (Okamura) Børgesen
Champia parvula (C. Agardh) Harvey	*Dictyota bartayresiana* J.V. Lamouroux
Champia vieillardii Kützing	*Dictyota dichotoma* var. *intricata* (C. Agardh) Greville
Hymenocladiaceae	*Padina jonesii* Tsuda
Asteromenia anastomosans (Weber-van Bosse) G.W. Saunders, C.E. Lane, C.W. Schneider & Kraft	**Fucales**
	Sargassaceae
Lomentariaceae	*Sargassum agaviforme* Tseng & Lu
Lomentaria corallicola Børgesen	*Sargassum hemiphyllum* (Turner) C. Agardh
	Sargassum henslowianum C. Agardh

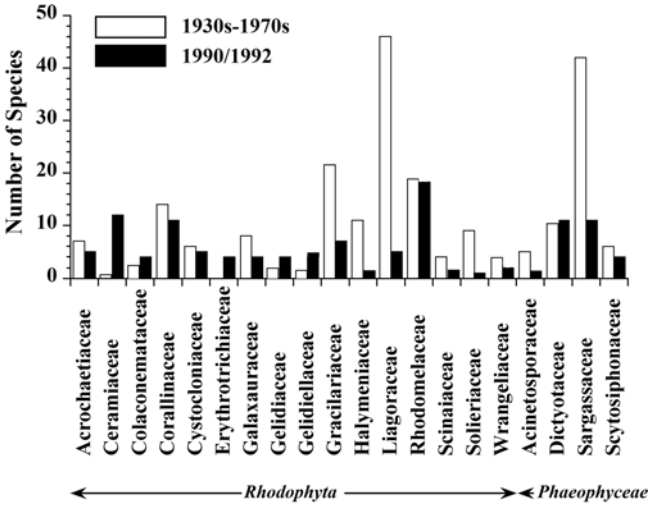

Fig. 2. Numbers of red and brown seaweed species in different families collected in Hainan Island during different periods. Comparison of species recorded during the early collection period (1930s–1970s) and the late collection period (1990/1992)

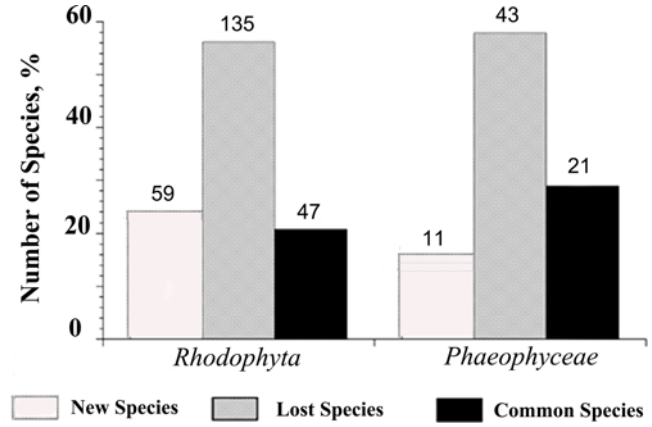

Fig. 3. Relative number (in % from the total number of species, EC+LC) of newly recorded species of red and brown algae for Hainan Island in 1990/1992, of species that had disappeared between the 1930s–1970s and 1990/1992, and of species common to both collection periods. Y-axis: Numbers are given in percentage of total species collected during time period from the 1930s to1990/1992, (EC + LC). Numerals above columns show species numbers common to both collections of lost species (not found in 1990/1992) and newly recorded species in 1990/1992

basic rules can be derived which have to be applied to obtain sound conclusions from the comparisons.

(1) Species lists should be derived from comparable collections which have been carried out at either annual or decadal intervals and in all relevant seasons. In this study, most of EC sampling was performed from late March to late June 1933 (for a period of about three months) and in January–February 1937 by C.K. Tseng. Small collections were also made by others in July 1934, August 1934 and December 1935, and all were included in the publications by Tseng (1935, 1936, 1937, 1938, 1941a, 1941b, 1942a, 1942b). Further sampling followed in June 1957, August 1960 and April 1980 (Chang and Xia 1963; Zhang and Xia 1991). There are two seasons in Hainan Island: a rainy season from April to November, and a dry season from November to April (Titlyanov et al. 2014a, 2014b). Therefore, the EC sampled during both relevant seasons and reflected the diversity and species composition of algae between the 1930s and 1980s.

The LC sampled at the end of both the rainy season (October–December 1990), and the dry season (March–April 1992), and so probably reflected the diversity and species composition of algae in the studied areas of Hainan Island during the period 1990–1992 with a high certainty. But as not all months were sampled in LC, a small amount of species with a very restricted occurrence time might have been under-sampled in LC.

(2) Algal sampling sites should cover the same geographical range as well as zonal features. The EC was carried out at 19 localities around Hainan Island (situated mainly on eastern and southern shores of Hainan). The LC was sampled at 16 localities, nine of which were common with the EC and were mainly situated on the southern and eastern shores of the island. Three localities were situated in the northwestern part of the coast and had not been investigated before 1990. In the both collections algae were mainly sampled in shallow waters from the splash zone to the lower intertidal and also from cast ashore material (Tseng 1936; Titlyanov et al. 2011a).

(3) In order to get a representative overview of the species diversity of a site, the main purpose of the study should be the description of the species composition. Studies which have a different purpose such as ecological, physiological or cultivation studies will not be representative of the local species diversity. The purpose of the EC and LC was namely the study of species diversity of the marine flora in Hainan Island (Tseng 1936, 2004; Titlyanov et al. 2011a).

(4) The sampling methods should ideally be the same and samples should be identified by highly qualified specialists. Both seaweed sample collections from Hainan Island were performed while walking or via snorkeling during low and high tides without the use of quadrates or diving equipment. The leading Chinese algologists C.K. Tseng, Chang J.F., Xia B.M., and others were the main collectors and taxonomists of the EC. The LC was sampled by Chinese and German

algologists under the guidance of Xia B.M. Herbarium samples of the LC were identified by specialists in tropical marine algae, namely B. Xia, T. Titlyanova and E. Titlyanov.

Changes in the marine flora of Hainan Island between the 1930s and 1990s

In a previous study (Titlyanov et al. 2011a) it was shown that considerable changes of green benthic marine algae of Hainan Island took place between EC and LC. Specifically, there was an increase in filamentous, tubular, and fine blade-like green algae, belonging to the families Cladophoraceae, Ulvaceae and a displacement of fleshy algae with a low surface to volume ratio, especially from the families Codiaceae and Caulerpaceae. These changes had been interpreted as a consequence of reef degradation and other environmental changes after 1980. The data presented here on brown and red macroalgae also show a considerable change in species diversity and dominant families and point in the same direction as described by Titlyanov et al. (2011a).

In all three algal groups, the species richness at Hainan Island decreased considerably in LC compared to EC. One hundred thirty-five, 43, and 28 species recorded in EC were not confirmed in LC in the red, brown and green algae, respectively (Titlyanov et al. 2011a; this study). On the other hand, many new species were found in LC, which accounted for 59, 11 and 37 species in the red, brown and green algae, respectively (Tables 1, 2 and 3; Titlyanov et al. 2011a). Thereby, the number of species with frondose and fleshy thalli with a low surface: volume ratio growing epilithically on hard substrata in LC decreased to about 62% of EC.

The greatest number of taxa with fleshy and frondose thalli which were not recorded again during LC was in the red algal family Liagoraceae (41 taxa), in the brown algal family Sargassaceae (33 taxa) and in the green algal families Caulerpaceae (8 taxa) and Codiaceae (7 taxa). Thereby the floristic composition altered drastically and many fine filamentous epiphytic algae which are highly productive and have a high surface: volume ratio appeared and increased more than four-fold (Tables 1 and 2; Titlyanov et al. 2011a).

One of the most likely reasons for this change between EC and LC is the degradation of the coral reef system surrounding Hainan Island.

The loss of many epilithic frondose species may be a consequence of the destruction of the coral reef carbonate structures by dynamite fishing, use of fossil and live corals for lime manufacture, constructions of piers and other coastal defences. This environmental degradation especially may have affected Sargassaceae which grow at depths of 1–3 m. Its species number decreased from 42 species in EC to 11 species in LC.

As documented by Titlyanov et al. (2011a) at many localities sampled in 1990 and 1992 the infralittoral/intertidal reef flats were characterized by dead or damaged coral colonies and their fragments. These habitat changes may have had an impact on macroalgal communities. A major effect of the dead and damaged coral colonies might be the provision of free substrate, which favors colonization of early successional species such as opportunistic green or red algae of the genera *Ulva*, *Cladophora*, *Chaetomorpha* (Titlyanov et al. 2011a), *Ceramium* and *Centroceras* (this study). These genera have been reported as early successional species occupying free substrate, and forming algal turf communities on coral reef ecosystems. They are also one of the most dominant epiphytes on coral reefs damaged by anthropogenic activities or natural catastrophes (e.g. Lapointe et al. 1997; Diaz-Pulido and McCook 2002; Sergeeva et al. 2007; Titlyanov and Titlyanova 2008; Titlyanov et al. 2008). Overall structural changes during environmental degradation are characterized by a decline in frondose marine algae due to their reduced competitive abilities for occupying free substrate compared to fine-filamentous forms (McCook et al. 2001; Titlyanov and Titlyanova 2008, 2012; Titlyanov et al. 2011a, 2011b). The comparison of EC and LC algal taxa performed here shows that in the EC approximately 50% of the species had frondose or fleshy forms while fine filamentous species represented the majority of species in the LC.

Pollution and eutrophication of the seawater (Titlyanov et al. 2011b), and withdrawal of edible and widely used marine plants in China and other countries of South-Eastern Asia (Tseng 1935, 1983, 2004) are also known to be a major factor for the loss of frondose marine algae. Biotic competition also influences the diversity and structure of algal communities. Herbivorous fish, some crustaceans and mollusks are known to change their diets following habitat changes (Clements and Choat 1993; Hughes and Seed 1995; Kennish et al. 1996; Cannicci et al. 2007). However, the influence of this factor might not be considerable as there has been constant overfishing in the shallow gulfs of Hainan Island (Zhang et al. 2006).

Some of the observed changes such as the marked reduction of calcified algae (Liagoraceae: decreased from 46 species in EC to only 5 species in LC) are difficult to explain by reef degradation alone. Thus, we also have to consider other

factors such as elevated water temperatures and/or ocean acidification. These climatically forced ecological changes have been documented over the past half century (Harley et al. 2012). Ocean acidification differentially affects seaweeds, depending on their carbon capture strategy (Hoegh-Guldberg et al. 2007; Hepburn et al. 2011; Harley et al. 2012). It has been suggested that the effects of ocean acidification on calcified species may be manifested as increased dissolution rather than reduced production of calcium carbonate (Roleda et al. 2012). However, we have no concrete evidence of the influence of ocean acidification on tropical algal assemblages. At the same time, laboratory experiments showed that enrichment of seawater with carbonic acid may have strong effects on all primary producers, including tropical seaweeds. Acidification negatively affects calcareous algae, evoking net dissolution of algal-derived $CaCO_3$ and sometimes leading to their bleaching and mortality (Anthony et al. 2008, Jokiel et al. 2008, Kuffner et al. 2008) and, therefore, it is not excluded from the list of possibilities that a nine-fold decrease in species richness of algae with calcified thalli from the family Liagoraceae is not only connected to the destruction of the coral reef and water pollution, but also with recent acidification.

5. Conclusion

The analysis of the floristic composition of the marine red and brown macroalgae of Hainan Island during different time periods revealed that considerable changes have taken place between the early collection period (1930–1980s) and the late collection period in 1990/1992. There was an overall increase in fine filamentous, tubular and blade-like red algae and a displacement of macroalgal species with a high volume to low surface ratio. This may be a consequence of reef degradation, increased urbanization and aquacultural wastes in shallow areas around Hainan Island, as well as global climatic changes such as acidification of seawater.

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